VALUING ECOSYSTEM FUNCTIONS: THE EFFECTS OF ACIDIFICATION*

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I. INTRODUCTION

Population growth and human territorial expansion is placing unprecedented burdens on the ecosystems of spaceship earth. Farmlands are being converted to suburbs, while forests are being converted to farmlands. The Amazon forest, earth's richest biological region, is losing to development each year an area half the size of Great Britian [Prance, (1977)]. Pollution is now recognized as a global problem with particular emphasis on acid precipitation and the greenhouse effect. Estimates of species lost to extinction worldwide are as high as 1000 per year [Myers (1979)].

But what values are reflected by this and similar data on our dwindling natural environment? A substantial part of the answer can come from a study of ecological systems placed in an economic framework. Ecological systems must be reduced to tractable analytical frameworks which can then be incorporated into economic models that are able to ascertain benefits and costs. For example, in environmental economics, studies have estimated the willingness to pay for trout fishing along a particular stream. These studies could be used to estimate the value of the effect of acid precipitation on trout populations. The trout have value to people, and if the trout were to vanish so would the benefits of the fishing. But the trout are only one species in a complex ecosystem. By removing other species, say certain insects that may appear to be of no value, the trout may also vanish. Thus, a proper valuation of an ecosystem entails not just the valuation of end products like trout, but a recognition of the interactions between the trout and other species so that the value of these other species can be established. By doing this, better estimates can then be made of the uncompensated costs associated with population growth and industrial expansion which affect the sources of pleasure and life support services that ecosystems provide.

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Ecosystems are incredibly complex. They may be composed of thousands of species interacting in either obvious or nonobvious ways. Each species fills a certain niche in the overall system, and depends on one or more of the other species for survival. But such a complex system is not foreign to economists. who have the difficult task of sorting out complex economies. Notions such as short-run and long-run equilibriums, steady states, and exogenous shocks appear to be applicable to both ecosystems and economies. In addition, the same type of questions arise in either system. For an economy, the economist uses models to determine the effect a tax in one sector has throughout other economic sectors. For an ecosystem, the ecologist (and the economist) may need to know the effect a particular pollutant that harms one insect species will have on all the other species.

The parallels between ecosystems and economics suggest that similar models may be used for each. Moreover, if this can be accomplished, then linking ecosystems with economies may be possible. Such a linkage would permit not only detailed descriptions of how a pollutant will effect an ecosystem, but how the changes brought about in the ecosystem will effect the economy and, in turn, how these changes in the economy will influence the ecosystem.

Ecologists have made attempts to answer such questions by using energy as a unit of value. By measuring the flow of energy through an ecosystem, one can determine how an exogenous shock might effect that energy flow [Grodzinske (1975)]. The effect is then evaluated using some pecuniary value placed on an energy unit. Some support for this approach could once have even been found among economists. The English economist, J.A. Hobson (1929) has remarked that:

"... all serviceable organic activities consume tissue and expend energy, the biological costs of the services they render. Though this economy

may not correspond in close quantitative fashion to a pleasure and pain economy or to any conscious valuation, it must be taken as the groundwork for that conscious valuation. For most economic purposes we are well-advised to prefer the organic test to any other test of welfare, bearing in mind that many organic costs do not register themselves easily or adequately in terms of conscious pain or disutility, while organic gains are not always interpretable in conscious enjoyment." (p. xxi)

According to one's perspective, Hobson's statement can be taken as support for an energetic basis of value, and as a plea for economists to devote much more attention to the workings of the biological world and its implications for human welfare, both as a source of pleasure and as a life-support system. Hobson's first point has been received warmly by ecologists such as H.T. Odum (1971), to the point where it has been enshrined alongside cost-benefit analysis as a means of evaluating proposed energy technologies [Energy Research and Development Agency (1975)]. However, it has been coldly received by modern economists. Georgescu-Roegan (1979) neatly expresses the economists' source of difficulty with energy as the unit of value for the satisfaction of human wants:

"The entropic nature of the economic process notwithstanding, it would be a great mistake to think that it may be represented by a vast system of thermodynamic equations.... The entropic process moves through an intricate web of anthropomorphic categories, of utility and labor above all. Its true product is not a physical flow of dissipated matter and energy, but the enjoyment of life. ...pleasure is not related by a definite quantitative law to the low entropy consumed." (p. 1042)

Thus the value of energy varies with its use. The correct approach is therefore to include the ecosystem in the economy where its use can be evaluated relative to all other goods.

Hobson's second point, that economics should give deeper consideration to the role of biosphere in human affairs, has suffered from neglect. With the exception of the work inspired by Boulding (1966) and Krutilla (1967), the economics discipline continues to be notable for its inability to capture

many of the concerns of biological scientists, particularly ecologists, about the impacts of human activities upon ecosystems and, via these ecosystem impacts, ultimately upon human welfare. Perhaps economists have dismissed these themes simply because the economics discipline has lacked a means of fitting them into the framework of economic analysis.

The purpose of this paper is to develop a link between ecosystem and economy that will allow an economic evaluation of ecosystem structure. We try to broaden traditional approaches to environmental economic problems by encompassing bioenergetics, but without resorting to the use of energy as the unit of value used by humans. There are two main phases of the development. First, an ecosystem model is described using the notions of production functions, optimization, and equilibria. Humans are absent from this phase. All energy input into the model derives from the sun. In the second phase, humans are introduced under the familiar guise of utility maximizer. This leads to behavior that interferes with the ecosystem through changes in the sources and uses of energy.

Section 2 develops a model of the optimizing behavior of a single organism in an ecosystsm. Section 3 extends this idea to multiple organisms and to ecosystem equilibrium. In Section 4, common ecological themes are discussed as they relate to the model. Human perspectives of the ecosystem enter in Section 5. Section 6 uses the developments of previous sections to address questions about the value of pollution impacts upon ecosystem structure. Section 7 is a simple general-equilibrium model incorporating the thoughts of previous sections.

II. OPTIMIZATION BY INDIVIDUAL ORGANISMS

Initially, we develop a model of an ecosystem where humans have neither a direct nor indirect influence. The model can be considered a depiction of prehistoric times or of very remote areas in modern times. In this world,

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all energy is derived from the sun.— Organisms may use this energy directly, in the case of plants, or indirectly, in the case of herbivores and carnivores. Each organism is a member of a particular trophic level, where a trophic level is defined as "...a collection of species which feed from the same set of sources and which do not produce for each other" [Hannon, (1976, p. 260)]. In essence, each trophic level can be thought of as a stratem in a food pyramid.²/ The objective is to link mathematically the trophic levels. This will provide a framework for discussing equilibria in the ecosystem.

Before deriving the links, however, the actions of the individual organisms must be described. In a general equilibrium model of an economy, individual consumers and firms are usually described as maximizers. But in an ecosystem, do nonhuman organisms maximize? Most people do not credit a weasel with thoughtful preference revelation when it raids the chicken coop instead of ferreting out a mouse or two. "...men consiously optimize, animals do not they survive by adopting successful strategies 'as if' conscious optimization takes place" [Hirschleifer (1977, p. 4)]. This "as if" assumption is sufficient to capture much of the behavior of nonhuman organisms, and, thereby, establish a fruitful model.

Various suggestions have been made as to what it is that nonhuman organisms maximize, or behave as if they are maximizing. Lotka (1925) developed a model where the maximand is the rate of increase of the species. This rate is a function of food capture, shelter, and other physical needs. Obtaining these needs requires energy expenditure, Naturally, if a species is to be successful, then the energy expended on the needs must be less than or equal to the energy acquired. Lotka characterizes a maximum in this system with a set of equations where the marginal productivity (i.e., an increase in the species) of an energy expenditure equals the marginal loss (i.e., a decrease in the species) from that energy expenditure.³/ Modern work has emphasized the role of energy

more directly in the search for a maximand. Odum (1971, p. 90) points out that life requires power and "...the maximum and most economical collection, transmission, and utilization of power must be one of the principal selective criteria..." Finally, Hannon (1976) develops a model using stored energy as the maximand. Stored energy is simply the energy aquired by the organism less the energy needed to maintain itself. Hannon argues for the reasonableness of this objective based on general observation, and on the increased organism stability it provides during periods of fluctuating inputs.

The stored energy approach is used here. It does not seem to differ significantly from Lotka's approach, particularly since he viewed organisms as energy transformers. As indicated in the next section, if organisms of a species are successful in storing energy, this is interpreted as leading to an increase in the species. Hence, the stored energy approach appears acceptable to modern ecologists, and consistent with the pioneering work of Lotka.

For specificity, suppose the organism is a fox which, as an energy transformer, gathers all its energy from food, and then assimilates this energy for various purposes. All input energy must be accounted for as output energy in the form of waste heat, metabolism, growth, reproduction, losses to predators, detritus, mechanical activities, and storage. Let x_i and ε_i', i=1 , ...n, be the mass flow from the ith source to the organism and the energy content per unit of mass i respectively. The x_i may be various species of small mammals preyed upon by the fox. Total input energy is then:

$$\sum_{i=1}^{n} \varepsilon_i' x_i \qquad (1)$$

Let ε_i'' be the energy spent to obtain a unit of x_i, so that the net input of energy from a unit of x_i is $\varepsilon_i = \varepsilon_i' - \varepsilon_i''$. Therefore, net input energy is:

$$\sum_{i=i}^{n} \varepsilon_i x_i \qquad (2)$$

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The energy outputs are given by x_k, $k = n+1,...,m$ and the energy content per unit of x_k is ε_k. For example, x_k may be the activity of searching for a den, and ε_k is the energy spent per unit of searching ng. For some inputs such as heat loss, x_k is measured in energy and $\varepsilon_k = 1$; however, no loss of general ity results from using ε_k. Total energy output is:

$$\sum_{k=n+1}^{m} \varepsilon_k x_k \qquad (3)$$

Stored energy is the difference between input and output. It represents energy in excess of what is needed for viability. Let r be this energy. Then, using (2) and (3):

$$r = \sum_{i=1}^{n} \varepsilon_i x_i - \sum_{k=n+1}^{m} \varepsilon_k x_k \qquad (4)$$

For convenience, all inputs and outputs will henceforth be denoted x_j, $j=1,...,m+n$, where $x_j > 0$ for inputs and $x_j \leq 0$ for outputs. Each $\varepsilon_j x_j$ is interpreted now as a net input of energy. Thus, if index j is heat loss, the net energy input from heat loss is $-\varepsilon_j x_j$. Expression (4) can be rewritten as

$$r = \sum_{j=i}^{m+n} e_j x_j \qquad (5)$$

The objective of the fox is to maximize expression (5).

A bundle of net inputs for the organism is represented by the m+n real numbers $x=(x_1,...,x_{m+n})$. Not all bundles are feasible for the organism. The fox cannot continually catch squirrels without ever losing heat energy. The set of feasible bundles will be called the physiology set.[4] In essence, this set places constraints on what is achievable for the organism by describing the physiological processes which convert inputs to outputs. For example, as a general rule of ecology, in order for the organism to use ingested material, it must oxidize the organic molecules in the material it ingests. [See Morawitz (1968, Chap. 5)]. This creates useful energy, but some formerly

useful energy is also lost as heat. The physiology set also will depend on ambient temperature, time of year, and other environmental conditions. Human activities may influence this feasible set. Acid precipitation is a good example of a human activity that interacts with an ecosystem via alterations in physiology sets.

A simple diagram illustrates these notions. Suppose for the fox there is only one input, squirrels, and one output, mechanical activity. Figure 1 shows the physiology set as the shaded region. The set is entirely within the second quadrant where squirrels are consumed in positive quantities and mechanical activity is a loss or a negative quantity. With mechanical activity of $\hat{x}_2$, the fox can attain a quantity of squirrels $\bar{x}$, a quantity $\hat{x}$, or any amount between $\hat{x}$ and the horizontal axis. Bundle $\hat{x}$ repesents the greatest amount of squirrels attainable for $\hat{x}_2$. For this reason, $\hat{x}$ is labelled an efficient point of the physiology set; and all points along the heavy curved border of the set are referred to as the physiologically efficient points.

Definition: A bundle $\hat{x} = (\hat{x}_1,\ldots,\hat{x}_{n+m})$ in the physiology set X is physiologically efficient if there does not exist an alternative bundle $x = (x_1,\ldots x_{n+m})$ in X such that $x_j \geq \hat{x}_j$, $j = 1,\ldots,m+n$, and $x_i > \hat{x}_i$ for at least one j.

Thus, a physiologically efficient bundle is one where greater amounts of energy cannot be attained without even greater losses of energy. Note that points along the nonheavy border in Figure 1 are, therefore, not physiologically efficent.

The dependency of the physiological set on environmental conditions is depicted in Figure 2. The cross-hatched area may represent the physiological set of a lake trout prior to the occurrence of acid precipitation, while the shaded region represents the trout's set subsequent to the acid precipitation. This change clearly indicates a detrimental effect from the pollution.
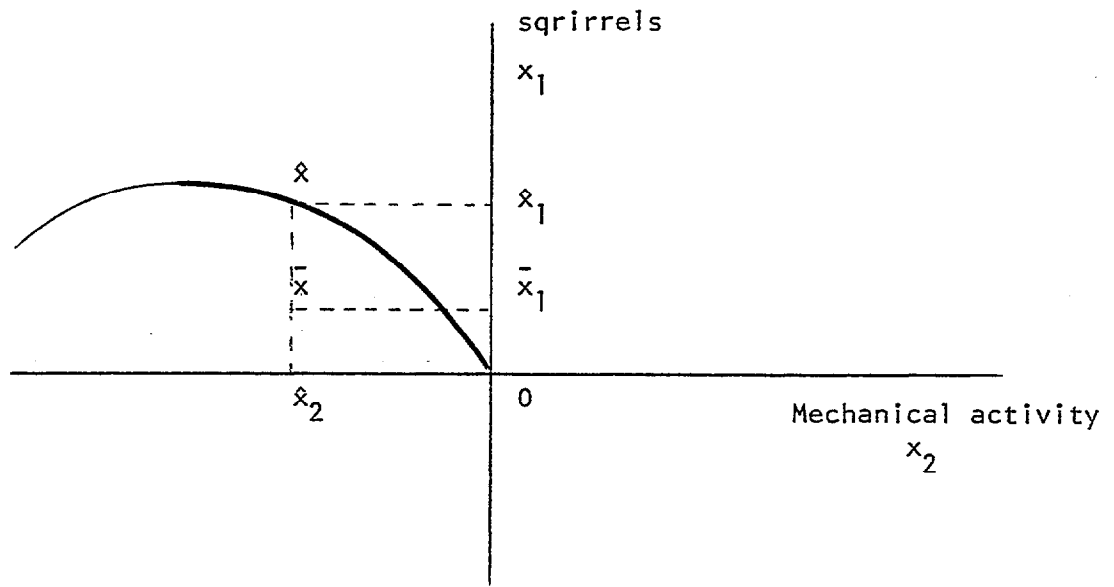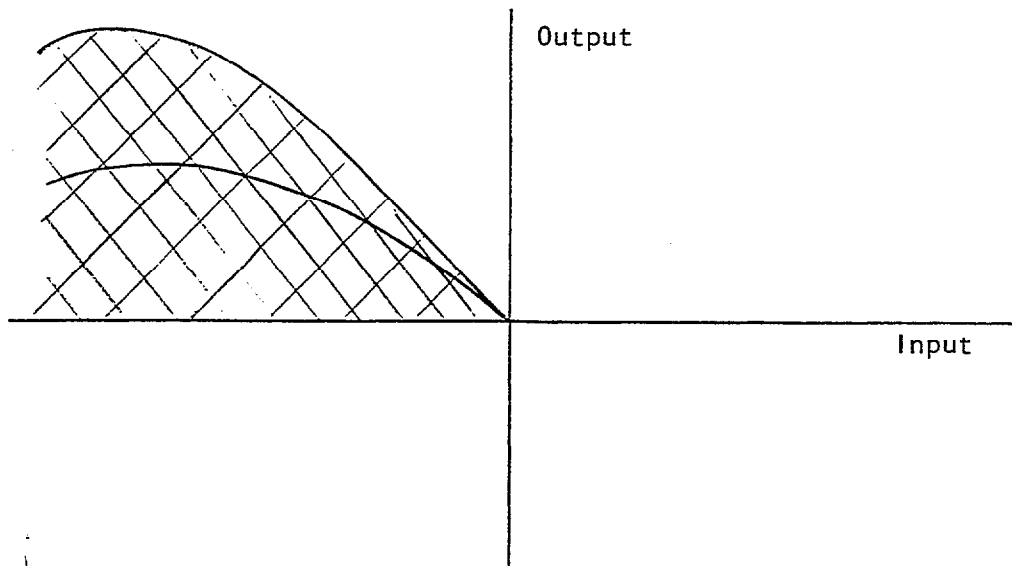
FIGURE 1

FIGURE 2

The fox behaving as a stored energy maximizer can be illustrated in the simple diagram as well. With one input and one output, the fox maximizes the expression from (5)

$$r \equiv \varepsilon_1 x_1 + \varepsilon_2 x_2 \tag{6}$$

For a fixed level of stored energy, $\bar{r}$, (6) can be plotted as the line in Figure 3 labelled $\bar{r}$. A higher level of stored energy is shown by the line $\bar{\bar{r}}$. The vertical and horizontal intercepts indicate the stored energy attainable, and the further the line from the origin in the first quadrant, the greater the stored energy. Given a particular point, say $\hat{x}$, and energies ε_1 and ε_2, the stored energy is given by $\bar{r}$. The slope of the line is the ratio $-\varepsilon_2/\varepsilon_1$, or the rate at which squirrels can be transformed into mechanical energy in the ecosystem. Thus, the ε_1's are the energy prices the fox faces.

FIGURE 3

$$x_1 = \frac{r}{\varepsilon_1} - \frac{\varepsilon_2}{\varepsilon_1} x_2$$
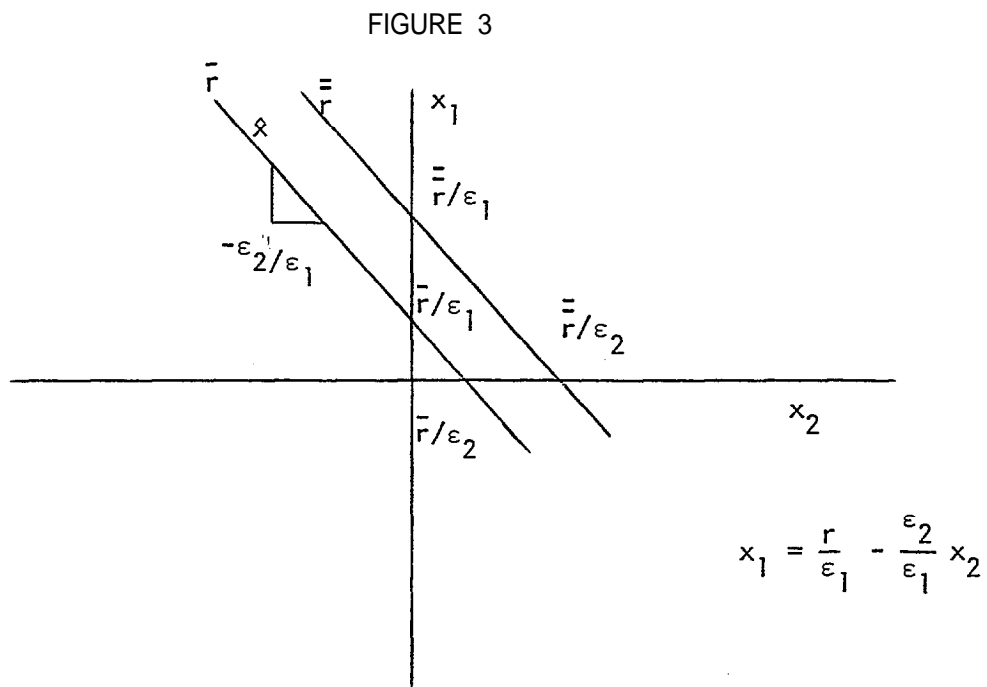
The fox is assumed to take ε_1 and ε_2 as given; that is, he has no control over these values. They are parameters in his maximization problem. The point of maximum stored energy will be given by that stored energy line that is furthest above the origin, but still having at least one point in common with the physiology set. Obviously, this point will be one that is physiologically efficient. Figure 4 illustrates maximums of $\hat{r}$ for values $\hat{\varepsilon}_1$ and $\hat{\varepsilon}_2$, and $\bar{r}$ for

FIGURE 4
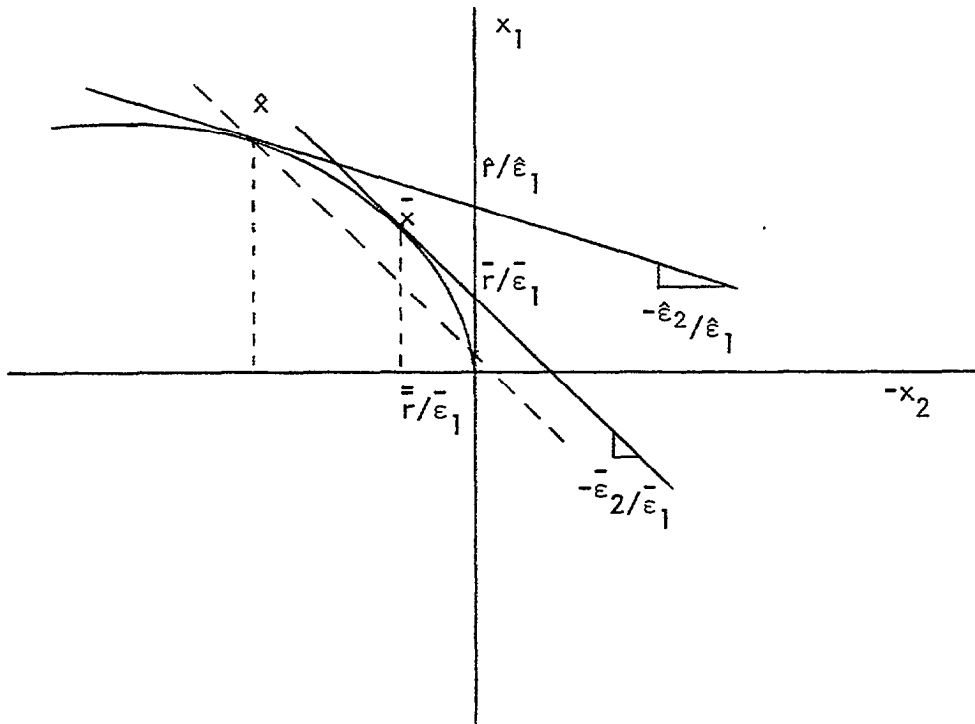
values ε_1 and $\bar{\varepsilon}_2$. The maximizing solution depends on the shape of the physiological set and the values of ε_1 and ε_2. At $\hat{x}$, greater levels of mechanical activity and squirrels prevail, because squirrels have more energy content $(\hat{\varepsilon}_1 > \bar{\varepsilon}_1)$ and/or mechanical activity results in less energy loss $(\hat{\varepsilon}_1 < \bar{\varepsilon}_1)$. For values $\bar{\varepsilon}_1$ and $\bar{\varepsilon}_2$, the fox would not move beyond point $\bar{x}$. To do so would mean more mechanical activity and more squirrels, but the energy gained would be less than the energy lost. Moving from $\bar{x}$ to $\hat{x}$ would mean a drop in stored energy from $\bar{r}$ to $\bar{\bar{r}}$.

A maximum will exist provided certain restrictions are placed on the physiology set. In particular, the set must be bounded and include its boundaries. These restrictions do not seem unrealistic n the real world. Figure 5 illustrates a set that is not bounded. For positive ε_1 and ε_2,

FIGURE 5
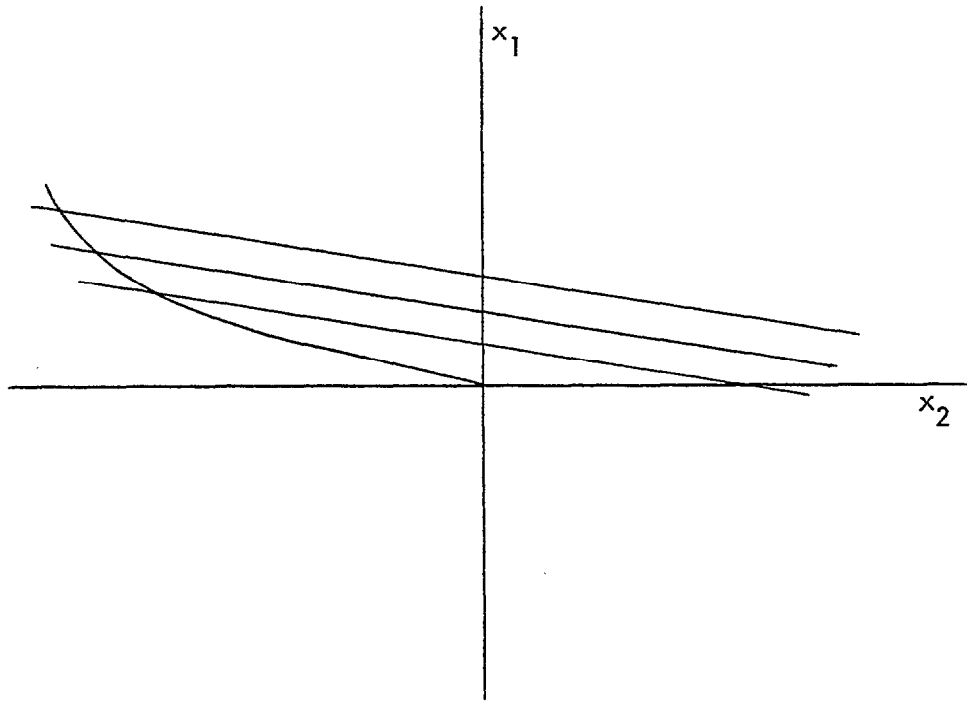
maximum stored energy is infinite. The shape of the set must be left to exper-

iments, observations, and statistical analysis, and it can be expected to vary

significantly among organisms. Research into these shapes is necessary

to apply the theory presented here.

Further insight into the maximization model can be gained by returning

to the general case with n+m variables. To do this, the concept of a physio-

logy function is introduced using the physiology set. For any set of values

of all but one of the net flows, x_j, ,there is only one value of x_j that is

compatable with physiological efficiency. This is obvious for the two variable

case from the figures above. For n+m variables, let $x^{-j} = (x_1, \ldots, x_{j-1},$

$x_{j+1}, \ldots, x_{n+m})$, then there is a one-to-one correspondence between the n+m-1

dimension vector x^{-j} and the scalar x_j. In functional form,

$$x_j = f(x^{-j})$$

or equivalently

$$F(x) = x_j - f(x^{-j}) = 0 \tag{7}$$

The function $F(x)$ is the physiology function, and, by construction, it embodies physiological efficiency. That is, $\hat{x}$ is physiologically efficient if and and only if $F(\hat{x}) = 0$, In two dimensions, $F(\hat{x}) = 0$ implies that $\hat{x}$ is on the border of the physiology set.

The maximization problem can be restated as

$$\max r \equiv \sum_{j=1}^{m+n} \varepsilon_j x_j$$

$$\tag{8}$$

$$\text{subject to} \quad F(x) = 0$$

where $F(x)$ is assumed to be twice differentiable and the physiology set is assumed to be strictly convex. Strict convexity assures that the second-order sufficiency conditions of the maximization problem are satisified, and that there is a unique maximum. The Lagrangian for problem (8) is:

$$L(x,\lambda) = \sum_{j=1}^{m+n} \varepsilon_j x_j + \lambda F(x) \tag{9}$$

and the first-order conditions for a maximum are

$$x_j: \qquad \varepsilon_j + \lambda \frac{\partial F(x)}{\partial x_j} = 0, \qquad j = 1,\ldots,m+n \tag{10}$$

$$\lambda: \qquad F(x) = 0 \tag{11}$$

Dividing any two conditions in (10) by each other yields

$$\frac{\partial F(x)/\partial x_i}{\partial F(x)/\partial x_j} = \frac{\varepsilon_i}{\varepsilon_j} \tag{12}$$

so that for a maximum, the rat o of partial derivatives of F(x) must be equal to the ratio of energy prices. Using (7),

$$F(x_1,\ldots,x_{j-1},f(x^{-j}),x_{j+1},\ldots,x_{m+n}) = 0$$

and differentiation with respect to x_i, $i \neq j$, yields

$$- \frac{\partial f(x^{-j})}{\partial x_i} = \frac{\partial F(x)/\partial x_i}{\partial F(x)/\partial x_j} \tag{13}$$

Thus, the left-hand-side of (12) can be interpreted as the rate at which x_j must be substituted for x_i while all other values are held constant. Or, for the foxe's predatory behavior, (12) states that the rate at which he can trade squirrels for rabbits while maintaining stored energy must equal the rate at which he can exchange squirrel energy for rabbit energy in the ecosystem.[6/] Alternatively, (12) and (13) can be used to obtain

$$- \frac{\partial \varepsilon_j f(x^{-j})}{\partial \varepsilon_i x_i} = 1 \tag{14}$$

The left-hand-side of (14) is the rate at which energy from source j must be traded for energy from source i in order to remain physiologically efficient. Or, substituting squirrels for rabbits must lower the input of rabbit energy at the same rate squirrel energy is increased.

The conditions for a maximum given by (12) can be related to the earlier figures.   Condition (12) for the one input-one output case is shown by the tangency in Figure 4. The left-hand-side of (12) is the slope of the physiology set border, and the right-hand-side of (12) is the slope of the stored energy line.

The first-order maximum conditions given by (10) and (11) constitute m+n+1 equations which can be solved for the optimum values of the x_i and λ

as functions of the energy prices. A solution is guaranteed by the assumption of a convex physiology set. Thus, there exist the functions:

$$x_j = \phi_j(\varepsilon) \qquad j = 1,\ldots,m+n \qquad (15a)$$

$$\lambda = \phi_\lambda(\varepsilon) \qquad (15b)$$

The function $\phi_j(\varepsilon)$ indicates the amount of the jth input acquired or j^{th} output spent, given the energy prices of all inputs and outputs. Substituting these amounts back into the objective function gives the maximum stored energy,

$$r = \sum_{j=1}^{m+n} \varepsilon_j \phi_j(\varepsilon) \qquad (16)$$

If j represents rabbits, $\phi_j(\varepsilon)$ can be thought of as the foxe's demand for rabbits at prices ε.

Finally, the $\phi_j(\varepsilon)$ terms can be substituted into (10) and (11), and derivatives can be taken with respect to the ε_j. This yields the system of equations:

$$1 + \sum_{k=1}^{m+n} \phi_\lambda(\varepsilon) \frac{\partial F(x)}{\partial x_j \partial x_k} \frac{\partial \phi_k(\varepsilon)}{\partial \varepsilon_j} + \frac{\partial \phi_\lambda(\varepsilon)}{\partial \varepsilon_j} \frac{\partial F(x)}{\partial x_j} = 0 \qquad (10')$$

$$j,k = 1,\ldots,m+n$$

$$\sum_{k=1}^{m+n} \frac{\partial F(x)}{\partial x_k} \frac{\partial \phi_k(\varepsilon)}{\partial \varepsilon_j} = 0 \qquad j = 1,\ldots, m+n \qquad (11')$$

This system can be used to solve for the $\partial\phi_k(\varepsilon)/\partial\varepsilon_j$ values, and, by the second-order conditions,

$$\frac{\partial\phi_j(\varepsilon)}{\partial\varepsilon_j} > 0 \qquad\qquad j = 1,\ldots, m+n \qquad\qquad (17)$$

The interpretation of (17) is that an increase in the energy price of a net input results in an increase in the use of that input. If the net energy the fox could obtain from a rabbit were to increase while the net energy obtained from a squirrel remained the same, the fox would chase more rabbits and fewer squirrels. A similar interpretation holds on the output side.

Before closing this section, a brief comparison between this model and economic models is worthwhile. The energy storage maximizing organism is analogous to the profit maximizing firm. The firm uses inputs (capital, labor, etc.) to produce outputs (guns, butter, etc.). The firm's technology set consists of net outputs, so that inputs are negative and outputs positive. This is opposite to the organism whose physiology set is made up of net inputs. Moreover, the firm pays money to buy inputs, and collects money in selling outputs. This also is opposite, since the organism collects energy from inputs, and pays energy for outputs. Inequality (17) is, however, the same for the firm and the organism since the two opposites cancel.

III. MULTIPLE ORGANISMS

An ecosystem comprises many stored energy maximizers which must be linked to provide a complete picture. Each individual organism belongs to a species, and sets of species form trophic levels. The trophic levels are links in a food chain or levels in a hierarchy. Each species feeds on species in lower trophic levels, and in turn provides food for species in higher trophic levels. Some hierarchies may be considerably more complex than others in that some

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species may interact with other species from many different trophic levels. At any rate, the fundamental idea is that the inputs and outputs of the previous section represent inputs from other organisms and outputs to other organisms.

At the bottom of the hierarchy are the simplest plants who derive all their input energy from the sun. In fact, in an ultimate sense, the sun supplies all the energy consumed by the ecosystem. This provides one equation in the ecosystem model: total output energy in the form of heat which is lost in the ecosystem equals total input energy from the sun.

By responding to the energy prices, ε, each organism behaves as the stored energy maximizer of the previous section. We assume each organism to be inconsequential with regards to its effect on the ecosystem, since there are so many other organisms. From this we infer that each organism has no control over the energy prices and thus takes them as given. This is consistent with the maximization process discussed above. However, the energy prices are determined overall by the activities of the organisms in the ecosystem. The foxe's energy price for acquiring rabbits will depend on the availability of rabbits. If an exogeneous shock were to reduce the number of rabbits drastically, we would expect the energy price to increase for the fox, causing a decrease in the foxe's stored energy.

The existence of an equilibrium ecosystem, given all the individual maximizers that are interacting, and given a set of initial conditions or initial numbers of organisms and environmental surroundings, requires the presence of a set of energy prices such that all organisms are maximizing stored energy while at the same time inputs are consistent with outputs and total energy is conserved. Existence will depend on the forms of the physiology sets and on any threshold conditions that may prevail. For instance, too few individuals of a certain species may lead to a total collapse of the species. There is also the possibility of multiple equilibria. That is, equilibrium,

if it exists, may not be unique. Different equilibria may consist of a variety of configurations of species numbers.

In accordance with Hannon (1976), stored energy is zero for all organisms in the equilibrium ecosystem. Recall that stored energy is energy above and beyond what is needed to survive. This is analogous to all firms making zero profit in a perfectly competitive economy. To see why this is, suppose an equilibrium exists and all species have zero stored energy; then consider an exogeneous change that causes foxes to have positive stored energy. The foxes are healthy, vigorous, and increasing in numbers. But this means that each fox will now face greater competion in his search for energy inputs. Numbers of rabbits will decline, and the energy price of rabbit inputs will increase. This increase will cause a decrease in the foxes' stored energy, until zero is again attained. A new equilibrium is established, although it may be one with more foxes and fewer rabbits than before. The same type of scenario can be used to show how the system responds to negative stored energies.

Setting up a mathematical model to study this ecosystem equilibrium is similar to the problem of setting up a general equilibrium, competitive model of an economy. The mathematics of existence can be complex, and will not be pursued here. However, efforts along these lines should be rewarding. Insights could be had regarding: 1) whether the stored energy behavior concept is consistent with observed equilibria; 2) those restrictions on the physiology sets consistent with equilibria and with field and experimental observations; and 3) the effects exogeneous shocks, such as human induced, acid precipitation, have on these equilibria.

IV.   COMMON ECOLOGICAL THEMES

Watt (1973, p. 34) sets forth the following as a fundamental principle of ecological science: the diversity of any ecosystem is directly proportional

to its biomass divided by its productivity. That is:

$$D = k\left(\frac{B}{P}\right) , \tag{18}$$

where D is a diversity measure directly related (Pielou, 1977, Chap. 19) to the number of species in a given habitat and the relative abundances of each species; [7/] B is the total weight or standing biomass of living organisms in a habitat; P is the amount of new living tissue produced per unit time; and k is a constant differing from one habitat to another. Thus, for a given biomass, system diversity and system productivity are inversely related.

Within a given habitat, d(B/P)/dt > 0, implying that in the early life of an ecosystem, the production of new tissue is very large compared to the amount of biomass. This high relative productivity is the source of biomass growth. It is achieved by introducing into an abiotic or stressed environment a small number of pioneer species (e.g., weeds) with rapid growth rates, short and simple life cycles, and high rates of reproduction. In the mature stages of an ecosystem, a wider variety of organisms that grow more slowly and have longer life spans is present. Net production or "yield" is lower in a mature system because most energy is invested in maintenance of the standing biomass. Thus, whereas energy in the pioneer stage is used to increase biomass, so that a relatively empty habitat can be filled, all the captured energy coming into a fully mature system is employed to maintain and operate the existing biomass, which already occupies all the habitat territory available.

Ecosystems that must live under intermittent or continued severe stress exhibit the attributes of immature systems: they have relatively low diversity, stability; and biomass but high throughputs of energy and thus high yields. The species present in these systems are refered to as generalists (Watt, 1973) because they are able to survive under a wide range of conditions.

Ecologists traditionally prefer ecosystems with large biomass and diversity. This preference for mature ecosystems appears to rest on two positions: the

maximization of system energy capture; and the maximization of system stability. In the first case, more energy is captured per unit biomass in a mature system because less energy has to be 'wasted" in growth and reproduction activities. The distinction is similar to Boulding's (1966) description of the "cowboy economy" and "the spaceship economy", where the former maximizes throughput and therefore energy diffusion, while the latter maximizes incoming energy concentration and fixation. According to Margalef (1968), the immature or stressed system expends more energy per unit biomass in reproduction in order to make up for its more frequent loss of individuals. In addition, because of its relatively small energy recycling capacity and its relative inability to alter and to renew its environment in ways favorable to its sustenance, it must expend relatively more energy per unit biomass in food gathering activities. The immature system thus expends relatively more energy in producing new tissue to replace that which has disappeared (depreciated). In contrast, the mature system expends most of its incoming energy in keeping what it has already developed: it is durable. Because it sustains a greater biomass per unit energy, the mature system is frequently said to be more "efficient" (B.P. Odom, 1971, p. 76).

Although exceptions appear to exist (Jorgensen and Mejer, 1979), the greater efficiency of mature ecosystems is associated in ecological thought with greater stability, where stability is variously interpreted to mean system resiliency to exogenous shocks or infrequent fluctuations in standing stock. This stability is thought to originate in a set of homeostatic controls present in greater number and variety in mature systems, thus providing a greater number of avenues through which the system can recover from damages to one or more of its components. The greater simplicity of the immature system increases the likelihood that if anything goes wrong, everything goes wrong. Thus monocultures which are by definition the simplest and least diverse of

ecosystems, are susceptible to being wiped out by any single pest or event to which they are sensitive. Incoming energy flows only through one or a small number of pathways; when this pathway is degraded, no means to capture energy remains. The system therefore collapses unless energy subsidies (e.g., fertilizers) are provided from outside. These subsidies are of course a further source of the low biomass supported per unit incoming energy that is characteristic of immature ecosystems.

The human dilemma posed by the ecologists then involves a tradeoff between high yield but risky immature systems with undifferentiated components, and low yield, reasonably secure systems with a variety of components. Even if the requisite energy subsidies were usually available, an earth covered with cornfields would be dangerous. Moreover, given, as Scitovsky (1976) convincingly argues, the human taste for variety and novelty, a world of cornfields would be exceedingly dull. Nevertheless, flowers and butterflies nourish only the human psyche; they provide little relief to an empty stomach. Human activities increase biological yields by accelerating energy flows through ecosystems. In terms of the model of the previous two sections, these activities increase overall energy prices. To accomplish this, they simplify ecosystem structures, either by keeping them in a perpetual state of immaturity or by impoverishing the energy flows their habitats can produce.

In the context of the above perspective, pollution, such as acid precipitation, harms human welfare by reducing yields of the material scaffold of wood, fish, and corn and by increasing ecosystem simplicity: yields are reduced and monotony is increased. Woodwell (1970) notes that by elimination of sensitive species, SO_2 air pollution around the Sudbury smelter in Ontario first resulted in a reduction in the diversity and biomass of the surrounding forest. Finally the canopy was eliminated with only resistant shrubs and herbs surviving the assault. He also notes that chronic pollution reduces

plant photosynthesis without having much effect upon respiration requirements. As a result, large plants, which have high respiration requirements, are placed at a disadvantage relative to small plants. In a vivid image, he posits the replacement of the great variety of phytoplankton of the open ocean by the algae of the sewage plants that are insensitive to just about any stress.

V.   VALUING DIVERSITY AND YIELD

In accordance with the treatments of Hannon (1979), Mauersberger (1979), and Sections II and III of this paper, the ecosystems refered to in the following development are long-run equilibria sustainable with various combinations of energy from solar, biogeochemical, and subsidy sources. Contrary to much of the ecological literature, day-to-day transient states in the relative abundances of various species are disregarded. This permits us to concentrate upon a small number of key expressions and basic principles, thereby avoiding the bewildering black-box flow diagrams often used by ecologists. We wish to gain insight into two questions. First, what is the economic value of the quantity of each species that a location is producing? For our purposes, a location is simply a set of map coordinates. Second, what is the economic value of the assortment or bundle of species that the location is producing? That is, what is the value of a particular ecosystem design? For a particular species assortment, the first question is usually answerable, given that market (not energy) prices of each species unit are readily observed or inferred. [8/] However, the second question, whether treated singly or in combination with the first, has not yet been grappled with insofar as ecological questions are concerned. We adapt a model of Lancaster's (1975) to deal simultaneously with the two questions.

To analyze these two questions, we need a model permitting us to trace through the impact upon the economic benefits derived from ecosystems of

changes in specie quantities and assortments caused by changes in energy flows. The first step in doing this is to define an ecosystem, e_i, as a set of species, where these species are in fixed proportions to one another. Expression (19) identifies ecosystem i with n species and

$$e_i \equiv (r_1^i, r_2^i, \ldots, r_n^i) \tag{19}$$

where r_j^i is the quantity of species j. Biomass is used to normalize the measure of different species. An ecosystem thus contains different species in a particular proportion at a single location. Ecosystems that contain species in different proportions are considered to be different ecosystems. Given the linearity of (19), the species content of x units of an ecosystem is simply x times the content of each species in an ecosystem unit.

Allow some time interval sufficiently long to permit each feasible ecosystem to attain a long-run equilibrium defined in accordance with the model of Sections II and III. Assume that a given amount of energy, $\bar{E}$, from solar, biogeochemical, and subsidy sources is available for this time interval at the location in question. Included in the biogeochemical energy source is the energy currently stored in the standing biomass. With $\bar{E}$, a variety of ecosystems can be established, the range of the variety being determined by the physiology sets of each species and the ways in which the species interact with each other.

Note that our notion of long-run equilibrium need not be a climax biological equilibrium; that is, it includes other sustainable states as well. In particular, by including energy subsidies and biogeochemical energy in available energy, we allow immature ecosystems to be formed and sustained. For example, an energy subsidy is being provided a vegetable garden when it is weeded and when it is harvested. The weeding prevents the garden from "revert-

ing" to field, woods or prairie; the harvesting prevents the standing stock of vegetable plants from suffering the effects of congestion. This standing stock will produce, period after period, a unique sustainable flow of new biomass or yield as long as the requisite biogeochemical energy and energy subsidies are provided. Similarly, with enough of an energy subsidy (as with a greenhouse) in Wyoming, one can sustain a banana-mango ecosystem with its associated flow of bananas and mangoes. We assume, whether reference is to an entire ecosystem or to a particular species within that system, that the sustainable yield measure is an order preserving transformation of the standing stock measure.

For a particular quantity of incoming energy, there will be some maximum amount of each ecosystem that a particular location can produce. [9/] Let the minimum energy requirements for producing an ecosystem be given by:

$$E = E(e(r)) = \phi(r), \tag{20}$$

where the elements of the r-vector are sustainable yields per unit time. $\phi(r)$ will be called a diversity possibilities function. It shows the maximum quantities of various species combinations that a location can sustain with given available energy each period. We assume that $\phi(r)$ is homothetic and convex, and that $\phi' > 0$. For a given energy flow at a particular location. Figure 6 illustrates a diversity possibilities function for grass and corn.

In Figure 6, four ecosystems are depicted, one of which, e_1, contains only grass, and another of which e_4, contains only COWS. Two ecosystems, e_2, and e_3, containing grass and cows in different combinations, are also depicted. If enough alternative ecosystems are possible, a continuous diversity possibilities

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FIGURE 6
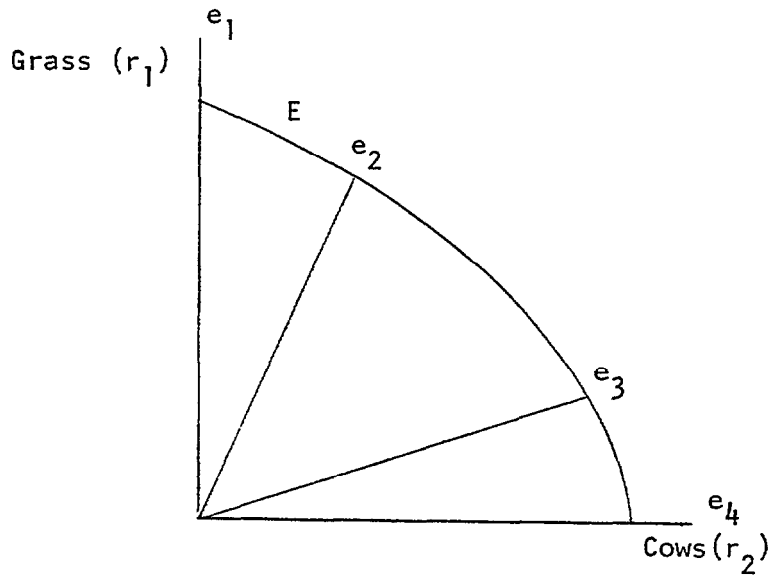
frontier, E, can be formed, as we assumed in (20). For given energy availability, each point on the frontier, E, represents the maximum quantity of one species that can be produced with a particular quantity of the other species being produced . Since cows probably use relatively less, if any, solar radiation directly, a progressive greater proportion of biogeochemical energy and energy subsidies will be included in E as one moves from the vertical axis to the horizontal axis.

The convexity of the frontier follows from an ecological version of the economic law of diminishing returns known as Mitscherlich's law [Watt (1973, p. 21)]. As progressively more energy is diverted from grass production to cow production at the location in question, the increment to the latter will decline. Similarly, the diversion of energy from cows to grass will result in

declining increments to grass production. Since in Figure 6, the cows could feed upon the grass, the convexity of the frontier is also attributable to the less biologically efficient use of the given available energy by cows than by grass. As a food chain lengthens, the amount of original energy used for production by species distant from the original energy input tends to decrease at an increasing rate (E.P. Odom, 1971, Chap. 3). Of course, as Tullock (1971) recognizes, the croppings and droppings of the cows may recycle some of the energy originally emobdied in the grass and cause both grass and yields to increase over some portion of the frontier. However, as grass becomes scarce, the cows must expend progressively more energy in search for it, if it is to remain a part of their food supply. Finally any cow grazing whatsoever might be so harmful to grass that the frontier bows inward, causing a nonconvexity problem for applications of economic optimization techniques.

The assumptions of homotheticity and $\phi' > 0$ for (20) imply that: $\phi(\lambda, r) = F(\lambda)\phi(r)$ for all λ, $r > 0$. In terms of Figure 6, these assumptions mean that there could exist a series of similar diversity possibility frontiers, one for each level of energy availability. The greater the level of energy availability, the farther would be the associated frontier from the origin. Therefore the biomass of any species obtained in a particular ecosystem to which greater quantities of energy are made available will increase but not necessarily on a one-to-one basis with the increase in available energy.

To make different ecosystems comparable, we define the solar radiation to which the location in question is exposed per period as the unit amount of energy, E_o^1. Each of the ecosystems that can be produced by this unit energy are therefore comparable in terms of the biomasses of each species embodied in them. We shall call them unit ecosystems. Keeping in mind that an ecosystem

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is defined as embodying species in fixed proportions, an altered quantity of an ecosystem is a simple multiple of the quantity of any species appearing to some positive degree in the unit ecosystem.

To complete the most fundamental parts of our analytical apparatus, we introduce a well-behaved utility function, U(r), for a representative person. Assuming any energy subsidies to the relevant location to be predetermined, the Lagrangian of this individual's decision problem then can be stated as:

$$L = U(r) + \mu(\bar{E} - \phi(r)).$$
(21)

The first-order necessary conditions for a maximum of (21) are,

$$\frac{\partial U}{\partial r} - \mu \frac{\partial \phi}{\partial r} = 0$$
(22)

and the constraint expressing the available energy. Expression (22) states that the individual will equate the marginal utility he obtains from an additional unit of a species to the marginal cost of expending the energy to acquire that additional unit. Figure 7 is a diagrammatic representation of (22) for two types of ecosystems, e_1, and e_2, and two indifference curves U_1, and U_2. With available energy, $\bar{E}$, the individual's utility-maximizing choice is clearly at A, which corresponds to (22). We shall therefore call any ecosystem which conforms to (22) the ideal ecosystem. This is the ecosystem having that species assortment most preferred by the individual.

Assume that our representative individual, perhaps because he is unable to exercise enough influence over land use, cannot have the e_1 ecosystem. Instead, he must face the e_2 system, a system containing substantially more cows and less grass. The latter system may be considered to be less "natural" since its maintenance likely requires substantial man-supplied energy subsidies. With the available energy, $\bar{E}$, the individual will be worse off with the

FIGURE 7

Grass (r_1)

e_1

A

B e_2

U_2

c

U_1

$\bar{E}$

E*

0   Cows (r_2)
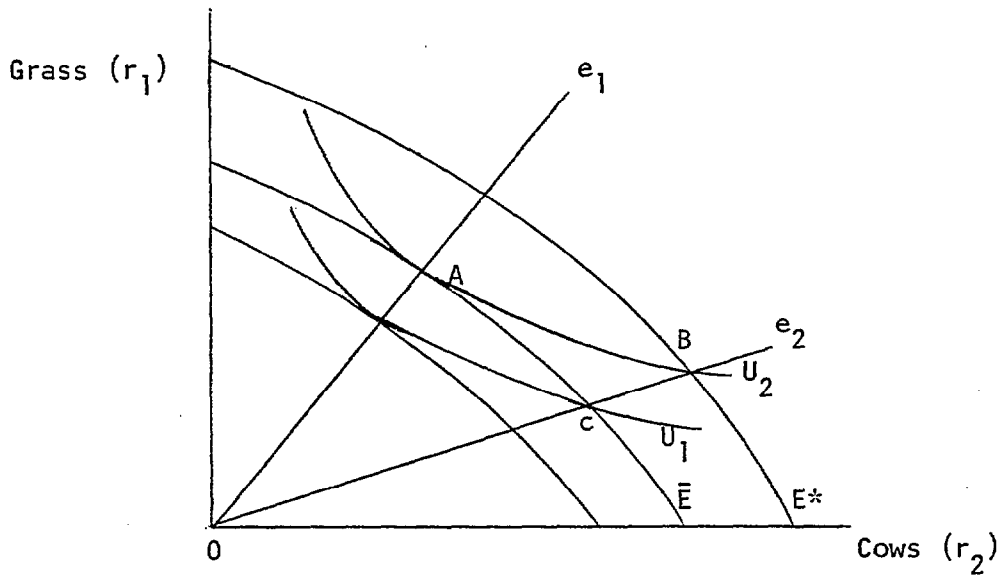
e_2 system since the highest utility level he will be able to reach is U_1 at

C. If he were to be as well off with the e_2 system as he would be with the

ideal system at A, he would have to be at B. The attainment of B, however,

requires more input energy as indicated by the diversity possibilities

frontier, E*. Since OA and OC both require $\bar{E}$ units of energy, while OB

requires E* energy units, the energy quantity required to compensate the

individual for the fact of the e_2 system is E* - $\bar{E}$ along the e_2-ray. The

compensating ratio, $\frac{OB}{OC} \geq 1$, is then the quantity of the existing system relative

to the quantity of the ideal system that keeps the individual at the original

utility level. Since OB and OC are each defined in energy units, the compensating

ratio is a pure number. A glance at Figure 7 makes it obvious that this

compensating ratio will be greater, the less substitutable the two systems

are for one another, the steeper the slopes of the diversity possibility

frontiers, and the wider the difference between the ideal ecosystem and the

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actual ecosystem. In addition to depending upon underlying preferences and production conditions, this ratio is obviously a function h(e,e*), where e* is the species ratio in the ideal ecosystem and e is the species ratio in the existing system. Lancaster (1975, p. 57) describes the properties of this compensating function, which must be convex.

If all existing ecosystems are not to be ideal ecosystems, the preceding framework implies that in the real world there are some ecosystems produced under conditions of increasing returns-to-scale. If decreasing returns-to-scale were universal, less energy would be used by producing fewer units of a greater variety of ecosystems. In the extreme, each individual would have his ideal ecosystem available to him. Similarly, under constant, returns-to-scale, the quantity of energy used to produce a quantity of an ecosystem is directly proportional. Thus, with decreasing or constant returns-to-scale, any individual who does not have his ideal ecosystem available is using more input energy to attain a particular utility level than would be required with his ideal ecosystem. Casual observation suggests that everyone is not happy with the ecosystems they have available. One plausible reason for this is the presence of increasing returns-to-scale in the production of ecosystems.[10] That is, the presence of increasing returns-to-scale for some ecosystems may force the individual to choose between an ideal diversity of ecosystem components and reduced energy consumption per unit of production for some smaller set of these components.

Let us momentarily return to (20), which gives the amount of input energy required to produce some amount of a particular ecosystem. Because of our use of energy to bring the unit quantities of different ecosystems to the same measure, and because of the properties we have assigned to the

diversity possibilities frontier, if Q_1, and Q_2 represent quantities of different ecosystems, e_1 and e_2, then $f_1(Q_1) = f_2(Q_2)$ when $Q_1 = Q_2$. This allows us to perform the analysis in terms of a single input function:

$$E = f(Q) \tag{23}$$

The energy required to produce quantity Q, of e_1 and quantity Q_2 of e_2 is given by the sum of the two input functions:

$$E = f_1(Q_1) + f_2(Q_2), \tag{24}$$

and not the sum of the quantities of $(Q_1 + Q_2)$. If $f_1(Q_1) + f_2(Q_2) = f(Q_1 + Q_2)$, then constant returns-to-scale would exist. As usual, we assume $f(Q) > 0$, and $f'(Q) > 0$, but we need not assume that all incoming energy results in additional biomass, nor need we attach any sign to $f''(Q)$.

Now define a degree of economies-of-scale parameter, $\theta(Q)$, which is the ratio of the average energy input requirement to the marginal energy input requirement. This is simply the inverse of the elasticity of (23), or:

$$\theta(Q) = \frac{f(Q)}{Qf'(Q)} = \frac{f}{Q} f' \tag{25}$$

If θ is a constant, $f(Q)$ will then have the form:

$$E = E_o Q^{1/\theta}, \tag{26}$$

the inverse of which is

$$Q = aE^\theta \tag{27}$$

This last expression is immediately recongizable as a homogeneous function of degree θ. If $\theta > 1$, there are increasing returns-to-scale; if $\theta = 1$, there are constant returns-to-scale, and if $\theta < 1$, there are decreasing returns-to-scale.

In expressions (21) - (22), we derived the representative individual's ideal diversity of ecosystem components, assuming that he faced no tradeoffs between this ideal and lowered unit energy costs of ecosystem production. We are now prepared to consider this question of the optimal deviation of

the actual ecosystem available to the individual from the individual's ideal ecosystem.

Assume we wish to enable the individual to reach some predetermined arbitrary utility level with minimum use of energy. [11] Let Q^* be the quantity of an ideal ecosystem, e^*, that is required for the individual to reach this predetermined utility level. If the available ecosystem, e, is nonideal, the individual will have to be compensated by being provided more than Q^* of the available system. According to our previous definition of the compensating function, $h(e, e^*)$, the amount of the available eco-system required to bring the individual up to the predetermined utility level will be $Q^*h(e, e^*)$. Since the input function (23) is independent of the species ratios (by the assumed homotheticity of production and the definition of unit quantities), the optimal ecosystem is that which minimizes the quantity, Q, required to reach the predetermined utility level. That is, we wish to minimize:

$$Q = Q^*h(e, e^*) \tag{28}$$

This minimum is given by:

$$Q^* \frac{\partial h}{\partial e} = 0, \tag{29}$$

which obviously corresponds to (22). This result is relatively trivial but it does serve as a necessary prelude to determination of the optimal deviation of the available ecosystem from the ideal ecosystem.

Suppose there are $n-1$ less-than-ideal feasible ecosystems, the deviation of each less-than-ideal system from the ideal system being given by $x_i = e^* - e_i$. Then the quantity of the ith ecosystem required to reach the predetermined utility level is given by: $Q_i = Q^*h(x_i)$. The total energy inputs required

to reach this utility level for all systems, whether ideal or not, are then:

$$E = f[Q*h(x_i)], \qquad (30)$$

where the x_i are the variables of the problem. From (30) is obtained:

$$\frac{dE}{dx_i} = Q* \frac{df}{dh} \frac{dh}{dx_i} = Q*f'h' \qquad (31a)$$

or

$$Q*h' = \frac{1}{f'}, \qquad (31b)$$

for a minimum expenditure of energy.

The interpretation of (31b) in economic terms is quite easy. The l.h.s. of the expression shows the increase in the quantity of the ith ecosystem required to maintain the predetermined utility level if there is a one unit biomass increase in the deviation of the available ecosystem from the ideal ecosystem. The denominator of the term on the r.h.s. shows the increase in the available quantity of the ith ecosystem to be obtained with a one unit increase in input energy. Thus (31b) says that the optimal deviation of the available ecosystem from the ideal ecosystem occurs when the change in the compensating ratio is equal to the reciprocal of the additional energy required to produce more of the ith ecosystem. As the available ecosystem deviates less from the ideal system, the compensating ratio decreases. If the energy inputs required to reach the predetermined utility level also decrease, then the ideal system would clearly be optimal. However, if the compensating ratio increases and, due perhaps to economies-of-scale in production with simplified ecosystems, energy inputs per unit of

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yield decrease, then the achievement of an optimum requires that the tradeoff between the two be recognized.

The optimum condition (31b) can be clarified when stated in elasticity terms. Upon defining the elasticity of compensating function as $\eta_h = \frac{xh'}{h}$ and substituting this and the elasticity, (23) of the input function into (31b), we have

$$\eta_h \left(\frac{h}{x}\right) = \frac{Q \cdot \theta}{f} , \tag{32}$$

which if f, h, and Q are fixed is simply

$$\eta_h(x) = \theta. \tag{32b}$$

Thus the optimal deviation of the available ecosystem from the ideal ecosystem occurs where the elasticity of the compensating function, $\eta_h(x)$, is equal to the degree, θ, of economics of scale in production. If x were such that $\eta_h(x) > \theta$, a one percent decrease in deviation of the available ecosystem would require η_h percent less in ecosystem quantity (remembering that all ecosystems are measured in the same units because they are defined relative to a unit ecosystem) and require $\frac{\eta_h(x)}{\theta} > 1$ percent less energy resources, so that energy inputs would be made smaller by reducing the extent of deviation from the ideal system. However, if $\frac{\eta_h(x)}{\theta} < 1$, an increase in the extent of deviation would reduce energy inputs. Thus when $\eta_h(x) = \theta$, the deviation is optimal. The welfare loss from an increase in the deviation of the available ecosystem from the ideal ecosystem is balanced by the increased ecosystem quantity obtained for a given energy input.

VI. THE IMPACT OF POLLUTION

In the previous section, we have presumed that over some interval of the input function, (23), there exists increasing returns-to-scale: that is, as more energy is devoted to the production of a particular ecosystem, the

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ecosystem yield per unit of energy is increasing. When there are feasible monocultural ecosystems that yield an output (e.g. beef) highly valued for consumptive purposes, or as an input (e.g., sawtimber) for a fabricated good, and if these ecosystems exhibit increasing returns-to-scale, then some deviation of the available ecosystem from the ideal ecosystem may be optimal. The condition for optimality is $Q*h'=(f')^{-1}$ or, in elasticity terms, $\eta_h(x) = \theta$. It is thus apparent that the extent of optimal deviation will vary with the parameters that influence the above conditions. The elasticity, η_h, is determined by the properties of the compensating function, h. The economies-of-scale parameter, θ, is either an exogenous parameter (with homogenous production) or is a function of yield, and thus of the compensating function.

Consider a pollutant, α, which might, in principle, effect h', f', or both. For example, a pollutant stresses ecosystems, making them immature, and thus less diverse. In addition, for at least some of the ecosystems remaining viable after the introduction of a pollutant, their yields are less than they would be without the presence of the pollutant, i.e., the level of ecosystem yield obtainable with any given provision of energy is reduced. Thus, in terms of Figure 7, the diversity reduction would be reflected in a rotation of the available ecosystem toward one or the other axes, while the reduction of yield of whatever ecosystem was ultimately available would register in a shift of the diversity possibility frontiers toward the origin. If the ideal ecosystem is unchanged, and if the reduction in diversity represents a movement away from this ideal system, then the individual will require additional compensation if he is to remain at the original utility level. A similar result occurs if f' (the additional

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energy input required to obtain an additional unit of an ecosystem) increases. In both cases, an increase in the deviation of the optimal from the ideal ecosystem occurs . The effect of a variation in α on the optimal deviation is easily found by differentiating either (31b) or (32b).

Upon differentiating (32b) with respect to α, we get:

$$\frac{dx}{d\alpha} = \frac{(d\theta/d\alpha) - (d\eta_h/d\alpha)}{(d\eta_h/dx) - (d\theta/dQ)} \tag{33}$$

Given the convexity of the indifference curves, the $\frac{d\eta_h}{dx}$ term in the denominator must be positive. If the degree of economics-of-scale is fixed or declines with increases in the level of output, the $\frac{d\theta}{dQ}$ term in the denominator must be negative. Thus the denominator in (33) will be unambiguously positive. The sign for (33) will therefore depend solely upon the terms of the numerator. If the ideal ecosystem has high diversity, the sign of $\frac{d\eta_h}{d\alpha}$ will be positive since the convexity of the indifference curve requires that reduced ecosystem simplification imply increased responsiveness of the necessary compensation to further simplification.

The sign of $\frac{d\theta}{d\alpha}$ in (33) is less easily determined. Remembering that $\theta = \frac{(f)f'}{(Q)}$, it is plausible that increases in α would increase only f', implying that $\frac{d\phi}{d\alpha}$ would be positive, but leaving the sign of the numerator in (33) dependent on the relative magnitudes of $\frac{d\theta}{d\alpha}$ and $\frac{d\eta_h}{d\alpha}$. It is of course possible that pollution would reduce the yields obtainable for every ecosystem for all output levels. This event would be reflected in a reduction in f, implying that $\frac{d\theta}{d\alpha} < 0$, for a given f' and Q. In this case, the increase in pollution would reduce rather than increase the optimal deviation of the available ecosystem from the ideal ecosystem!

These results obviously imply that economic analyses which concentrate only on the ecosystem yield effects of pollution can be seriously misleading.

In cases where pollution reduces both yields and diversity, the analyses will tend to underestimate the economic losses from the effects. Similarly, if there exist cases where diversity is decreased while yields are increased, the usual analyses might not perceive any losses. However, in some cases, the usual analyses will exaggerate the severity of the losses. Harkov and Brennan (1979 pp. 157-158) conclude, for example, "...that slower growing trees, which often typify late successional communities, are less susceptible to oxidant damage than rapid-growing tree species, which are commonly early successional species." Assuming that the ideal ecosystem is more diverse than was the available ecosystem before the increase in pollution, the increase in pollution could reduce f', θ, or both. In either circumstance, more incoming energy would be required than before to obtain a given yield with the immature ecosystem. The pollution may therefore reduce the optimal deviation of the available ecosystem from the ideal system. In short, pollution can enhance rather than hinder the willingness of individuals to live with mature biological communities! Obviously, in this case, any economic analysis which neglected the increase in diversity would over-estimate the economic damages attributable to the pollution.

VII. A SIMPLE GENERAL EQUILIBRIUM MODEL

A simple general equilibrium model of an economy and ecosystem will now be presented that in some respects captures more dimensions of our basic concerns than do preceding sections, but which does so at the cost of neglecting some dimensions that the preceding sections feature. The ecosystem will be represented by the single stored energy variable r. Of course, this masks many interesting questions (e.g. diversity vs. scale economies) due to the

level of aggregation taking place. Nevertheless, the ecosystem solves the one-input problem

$$\text{max } r = \varepsilon_1 x_1 - \varepsilon_2 x_2$$
$$\text{s.t. } x_2 = g(x_1; E_r) \tag{34}$$

where E_r is a parameter indicating the amount of human supplied energy into the ecosystem. In Section II, we saw that $E_r = 0$. The solution to the problem is characterized by the first-order condition,

$$\frac{\varepsilon_2}{\varepsilon_1} = \frac{\partial g(x_1; E_r)}{\partial x_1} \tag{35}$$

This is the analogue of (12). If the ecosystem is in equilibrium, with no human interaction (i.e., Er = 0), r=0.

In order to capture a general equilibrium setting, we now introduce a Hicksian composite good, z, into the individual's utility function. Thus human preferences are given by:

$$U(z,r) \tag{36}$$

The term r appears in the utility function to indicate the human preference for a natural environment. Ideally, that environment should be pollution free with little trace of intervention. In other words, for some z value, zero is an optimum value of r. As intervention increases through increased Er, r increases and utility decreases for fixed z. Consumer preferences are shown by the indifference curves of Figure 8. The arrow shows the direction of preference.

The production of z is given by the function

$$z = f(E_z, r) \tag{37}$$

where E_z is the energy used in the production of z. Stored energy enters z
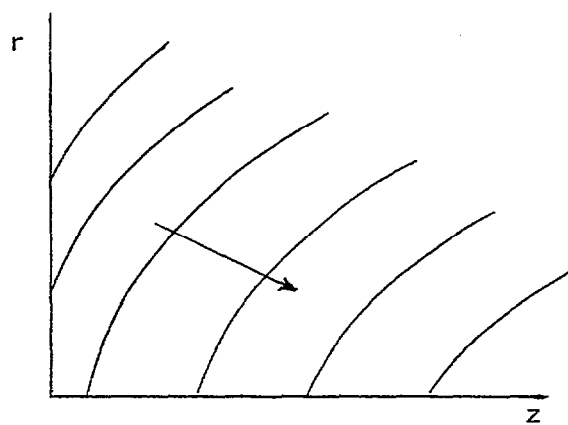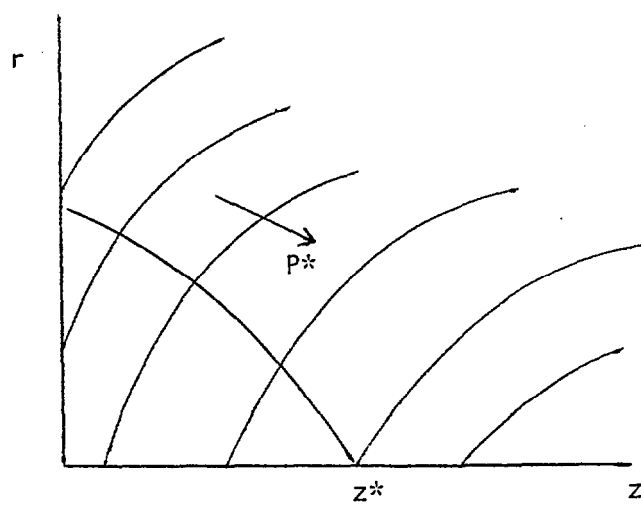
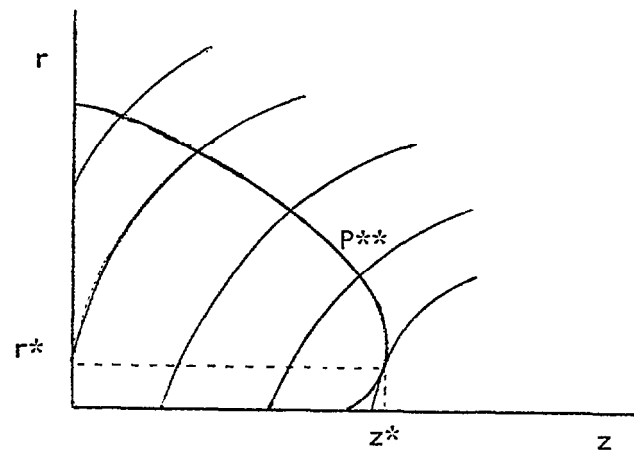## FIGURE 8

FIGURE 9

FIGURE 10

since it represents that part of the ecosystem which is cropped to provide goods in the economy.

The human problem is to maximize (36), subject to (35), (37), and the resource constraint on total available energy.

$$E_r + E_z = \bar{E} \tag{38}$$

The solution is shown graphically by the two possibility curves in Figures 9 and 10. In Figure 9, curve P* is the production possibility frontier. As we move from z*, incoming energy is being diverted from the production of z to r, and, therefore, more r is produced. Greater r means more natural environment is available for producing z. However, the shape of P* indicates that the increase in r does not make up for the decrease in E_z in the production of z. The optimum is z* where the ecosystem is in a natural state.

The second possibility is curve P** in Figure 10. Again, energy is being diverted to r. But now in producing z, the increase in r more than makes up for the loss of energy E_z as shown by the shape of P**. The optimum is now r**, z** where intervention in the ecosystem is justified. Examples of these possibilities may be forest harvesting since most everyone would agree that harvesting forests for lumber is a worthwhile task. The first case may be harvesting baby harp seals, since many argue that the goods made from the seals can made be inexpensively using synthetics.

While this is a very simple example, it is a useful means of displaying the potential for describing the links between economies and ecosystems. Questions of optimum exploitation and extinction can be inferred from sophisticated versions of the analyses in Figures 8 through 10. But research is needed to determine the shape of the possibility frontiers, which means that research into physiology sets of ecosystems and the technology sets of economies will be required.

VIII. SUMMARY AND CONCLUSIONS

We have tried to demonstrate how the application of economic analysis to bioenergetics, a framework with some degree of acceptance in ecology, can be used to describe the behavior of ecosystems. Moreover, we have indicated how the descriptions thereby obtained can be made an integral part of a model adapted from Lancaster (1975) that, in principle, can be used to value both the yield and the diversity impacts of stresses upon ecosystems. We are by no means the first to express the thought that the human-induced ecosystem effects for which one may feel secure using the conventional methods of benefit-cost analysis may be those having the least long-term economic significance. The conventional analysis disregards caddisflies because their contribution to the food supply of trout has been untraceable. We believe further attempts to combine bioenergetics and economic alaysis might make this view untenable. Neglect of the life support services that caddisflies and their peers provide for trout may mean that the ultimate effects of pollution on trout, via caddisflies, may go unrecognized and therefore unaccounted.

Just as the conventional analysis disregards the life support services provided by soil microbes, dung beetles, and caddisflies, it focuses upon an (incomplete) item-by-item listing of organisms in the ecosystem while failing to consider how the proportions in which these organisms are present might be sources of human pleasure. The ecologist, even though he has lacked an acceptable means to value ecosystem diversity, seems to have been more sensitive to this source of welfare than has the benefit-cost analyst. Economic efficiency, narrowly interpreted as minimizing the inferred or observed cost of producing a given quantity of ecosystem yields (and thereby

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taking advantage of all scale economies), need not result in maximum human welfare if there exists diversity in tastes among individuals for types of ecosystems. We speculate that traditional benefit-cost analysis, to the extent that the information it generates has been used for decision purposes, may occasionally have fostered Pareto-losses rather than Pareto-improvements. At a minimum, it has probably brought about wealth transfers from those who value ecosystem diversity and variety to those who possess the machinery for producing and maintaining ecosystem homogeneity.

1/ This ignores other possibilities like geothermal systems or tides.

2/ This is somewhat simplified in that it ignores more complex chains.

3/ Lotka likens the development of this model to the work of Jevans and the
marginalist school of economists. He regognizes that this maximal is not
appropriate for humans. Borrowing from Pareto, he describes humans as
maximizers of pleasure. This is consistent with maximizing species growth
only if the marginal pleasures (i.e., marginal utilities) are proportional
to the marginal productivities of the physical needs. Thus, Lotka essen-
tially denies the validity of an energy theory of value which, as pointed
out earlier, has been propounded by many modern day ecologists.

4/ The physiology set is analogous to the firm's technology set often used
in economics. The development of the model presented here closely parallels
the development of the economic model in Russell and Wilkinson (1979, Chapter
7).

5/ This is paraphrased for Russell and Wilkinson's (1979, p. 129) definition
of technologically efficient bundles.

6/ Condition (12) is analogous to the geometric solutions of Rapport (1971)
where he determines the optimum selection of two different preys. His
indifference curves represent two net inputs and one net output in the
model used here.

7/ The numbers of a particular species are capable of interbreeding.

8/ See Freeman (1979) for a thorough survey of available techniques
for answering this question.

9/ The work of Bigelow and his colleagues (1977) is a detailed account
of the ecosystem possibilities in a Dutch estuary. Odom (1971) and
other ecology texts are replete with other examples.

10/ Other plausible reasons exist. For example, a process through
which the individual can register his ecosystem preferences may be
lacking.

11/ The envelope theorem (Shephard's lemma) assures us that the solution
to this problem is equivalent to the solution of the utility maximization
problem.

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